Harvesting Impacts on *Macrocystis integrifolia* : A Preliminary Study

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HARVESTING IMPACTS ON *MACROCYSTIS INTEGRIFOLIA:* A PRELIMINARY STUDY

by

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ABSTRACT

The impact of harvesting on growth of the giant kelp, *Macrocystis integrifolia* Bory, was studied in a large, medium density kelp bed near Masset, B. C., in the Queen Charlotte Islands. Standard growth rates, G (growth in cm/day of a 1m frond) for control (unharvested) plants in June were 5 - 6 cm/day for plants at the outer edge of the bed, 4 - 5 in the middle of the bed, and 3 - 4 at the inner edge. During July respective G values were 4.5 - 5.5, 5 - 6, and 4 - 5. At all positions G dropped below 4 during August and September. Harvesting at 1.6 m below mean water level in early June significantly lowered growth rates, however growth rates after harvesting in mid July were not significantly effected and may have been slightly enhanced. Inner bed plants tended to have more blades per length of stipe than outer plants; this parameter was not effected by harvesting. Blade initiation rates were similar throughout the bed ($\bar{X}$ = .28 blades/day from June-September) and were not significantly effected by harvesting. Two methods for the estimation of canopy replenishment time following harvesting are described and compared.

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INTRODUCTION

Macrocystis integrifolia Bory is a large kelp which forms dense beds along portions of the outer coast of British Columbia (Field and Clark, 1978). It has considerable economic potential as a source of algin, as a mineral supplement for humans and livestock, and as a fertilizer base (Druehl, 1972; Whyte and Englar, 1974, 1976, 1978; Whyte et al, 1976). Long term industrial utilization of *Macrocystis* will require that wild stocks regrow and recruit following harvest. Thus, survival of a kelp industry will depend on the development of sound resource management guidelines to ensure conservation of the resource base. Such guidelines must be based on an understanding of how *Macrocystis* grows and reproduces, and how these phenomena are influenced by the natural vagaries of the environment and the added pressure of harvesting by man.

While the basic pattern of frond initiation and growth of *Macrocystis* have been known for some time (Scagel, 1947), the actual rate of frond growth has been observed infrequently. Scagel's (1947) pioneering study near Port Hardy, B.C. provided the earliest published growth rates for *Macrocystis* in British Columbia. The only other published records are those of Lobban (1976, 1978a, 1978b) who studied growth and translocation in Barkley Sound, B.C. Growth rates of *M. pyrifera* in southern California have been reported by North (1968, 1971). Frond growth rates following harvesting have only been reported for *M. pyrifera* (North, 1968).

Several regions of the Queen Charlotte Islands, in the north coastal waters of British Columbia, have extensive beds of *Macrocystis* having potential economic value (Coon et al, 1979). This report contains the results of a preliminary study of harvesting impact on the regrowth of *Macrocystis* in McIntyre Bay, off the north coast of Graham Island (Figure 1). It provides the first record of *Macrocystis* growth information north of Vancouver Island. Frond growth and blade initiation

rates were examined as effected by harvesting, time of harvest, and the position of plants within the bed. A preliminary analysis of canopy replenishment rate is provided as an exercise to illustrate the use of the abovementioned data types as predictive tools for the resource manager.

HISTORICAL NOTES

The beds of *Macrocystis integrifolia* Bory and *Nereocystis luetkeana* (Mertens) Postels and Ruprecht off the north coast of Graham Island constitute one of the larger concentrations (Coon *et al*, in prep.) of readily accessible kelp in the coastal waters of British Columbia. Yet the first commercial interest in the Queen Charlotte kelp resources emerged only in 1967 when Canada Kelp Company Limited applied for harvesting licences for the whole of the Queen Charlotte Islands. Since the Queen Charlottes were not surveyed in the 1946 inventory of B.C. kelp resources (B.C. Research Council, 1947), Canada Kelp conducted its own inventory in August and September, 1967 (Norpac, 1968). Bed areas, densities and total biomass were estimated between the Mazarredo Islands in Virago Sound and the Kliki Damen River just east of the mouth of Skonun River (Figure 1) An estimated total standing crop of 140,630 tonnes (72,849 tonnes of *Nereocystis* and 67,781 of *Macrocystis*) were located in the survey area

In 1968 Canada Kelp completed construction of a drying plant near Masset with the aim of supplying kelp meal to the European and Japanese markets. A 1,000 ton per day capacity harvesting vessel was under construction when the company, through a financial setback, was placed in receivership. In 1972 the complete assets of Canada Kelp were acquired by Kelpac Industries Limited and, in August, 1973, the drying plant first produced kelp meal in a trial run operation (Whyte and Englar, 1974).

In 1973 the Marine Resources Branch and the Industrial Development Division of the Federal Fisheries and Marine Service jointly funded another inventory of kelp stocks to cover the areas previously inventoried (Blakely and Chalmers, 1973). Aerial photography using 70 mm false color infra-red film was employed to determine bed areas for each species and ground truth sampling to estimate bed densities (kg/m^2). Total standing crop biomass was estimated by multiplying area X density. An estimated total standing crop of 117,235 tonnes (*Nereocystis* - 48,819 tonnes; *Macrocystis*

68,416 tonnes) was found in the survey area.

Kelpac was unable to secure its financial base in time to put the Masset plant into operation for the summer of 1974, but expected to be in full scale operation by June, 1975. This year-long interum period allowed for the initiation of a kelp management research program. The results of this preliminary research form the body of this text. Kelpac's development plan never came to fruition, and, as of 1979, no further harvesting studies have taken place in this region. *Macrocystis* biomass in the Masset area was reassessed in 1976 and 1978 (Coon *et al*, 1979; Coon *et al*, in prep.), using the inventory method developed by Foreman (1975).

DESCRIPTION OF STUDY SITE

The study site was a moderately dense *Macrocystis* bed located off South Beach in McIntrye Bay (54° .03' N, 132° .6' W) at the northern end of Graham Island in the Queen Charlotte Islands, British Columbia (Figure 1). The bottom was sandy near shore and changed to firm clay 800 m from the shore. *Macrocystis* grew on boulders scattered throughout this region from approximately 3 m below MWL near shore, to 6 m below MWL at the outer edge of the bed. Mean water level for 1974 was 2.9 m. Tidal range during large tides is 6.0 m; HHW is at 6.0 m above datum and at LLW is at 0.0 m. Temperature and salinity at 0.9 m depth were reported by Giovadi and Hollister (1973) for nearby Langara Island in 1973. Temperature increased from 9.3°C in June to 11.7°C by September, and winter temperatures were 6 - 7°C. Average monthly salinities throughout the year varied by no more than 1 °/oo from 32 °/oo. Mean hours of bright sunshine per month over six years for Sandspit (Figure 1) from June through September was 174, and November through February was 67 (Department of Agriculture, 1972). The study site was exposed to waves and surge during spring and summer; the senior author has observed that the bed is thinned considerably over the winter months.

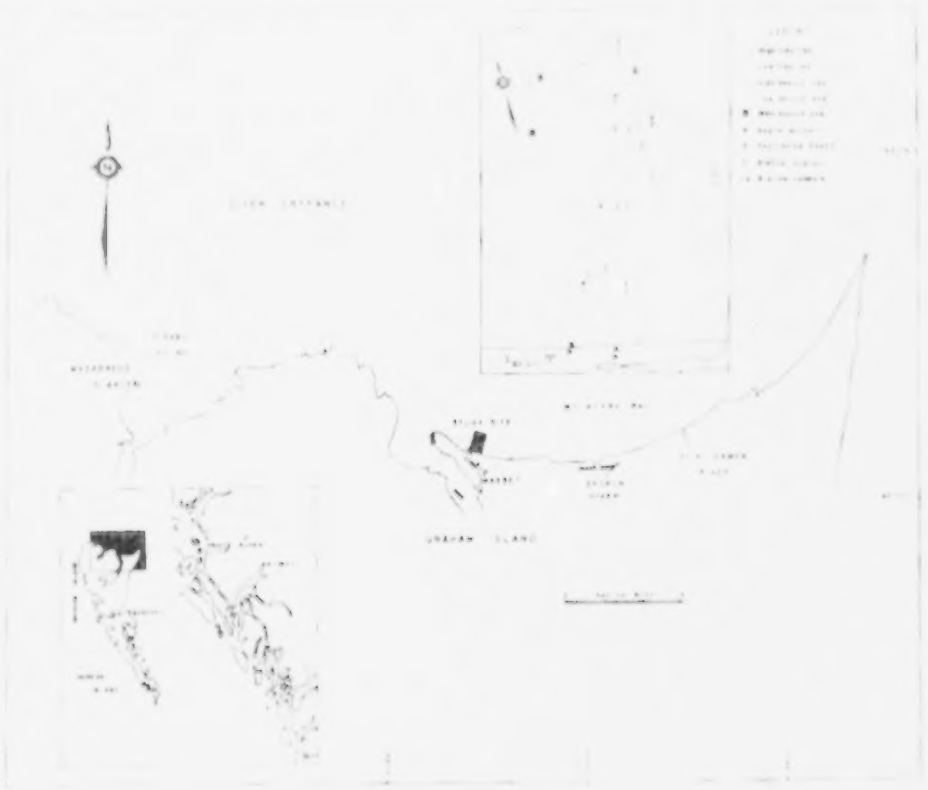


Figure 1. Location of the *Macrocystis* harvest study site near Masset, Q.C.I., in summer 1974. Bed density information is from Coon *et al*, (1979).

DESCRIPTION OF *MACROCYSTIS INTEGRIFOLIA*

The giant kelp *Macrocystis integrifolia* grows attached to rock substrate only in areas with little seasonal variations in sea water temperature and salinity or in areas where lower salinities occur during winter when water temperatures are low (Druehl, 1978). Druehl's observation that the distribution of *Macrocystis* in Barkley Sound is restricted to moderately wave-exposed areas or areas subjected to appreciable tidal currents (provided solid substrate is available) can, on the basis of the senior author's experience, also be generally applied for the rest of the British Columbia coast.

Macrocystis exhibits a determinate heteromorphic alternation of generations, with a microscopic oogamous gametophytic stage and macroscopic sporophyte stage. Sporophyte plants produce asexual unilocular sporangia in soral patches on specialized basal laminae called sporophylls. Mature sporangia rupture, releasing biflagellate, motile zoospores which, after settling on suitable substrate, lose their flagella and develop into male or female gametophytic branched filaments. Male gametophytes develop antheridia that liberate motile biflagellate sperm. The females extrude a large egg cell which develops into an embryo after fertilization. The zygote undergoes repeated divisions, producing a small stipe and blade. This juvenile sporophyte grows rapidly and ultimately results in the mature sporophyte. Under good illumination in shallow water, about one year is required from zoospore liberation to the development of a mature sporophyte, representing the completed life cycle of *M. pyrifera* (Neushul and Haxo, 1963). We estimate that about the same time period is required for *M. integrifolia* to complete its life cycle in British Columbia waters.

Details of the morphology and growth of the sporophyte of *M. integrifolia* are provided by Scagel (1947) and Lobban (1978a). The blade of the juvenile sporophyte divides dichotomously to form two identical blades; while still dividing dichotomously, each half begins dividing unilaterally

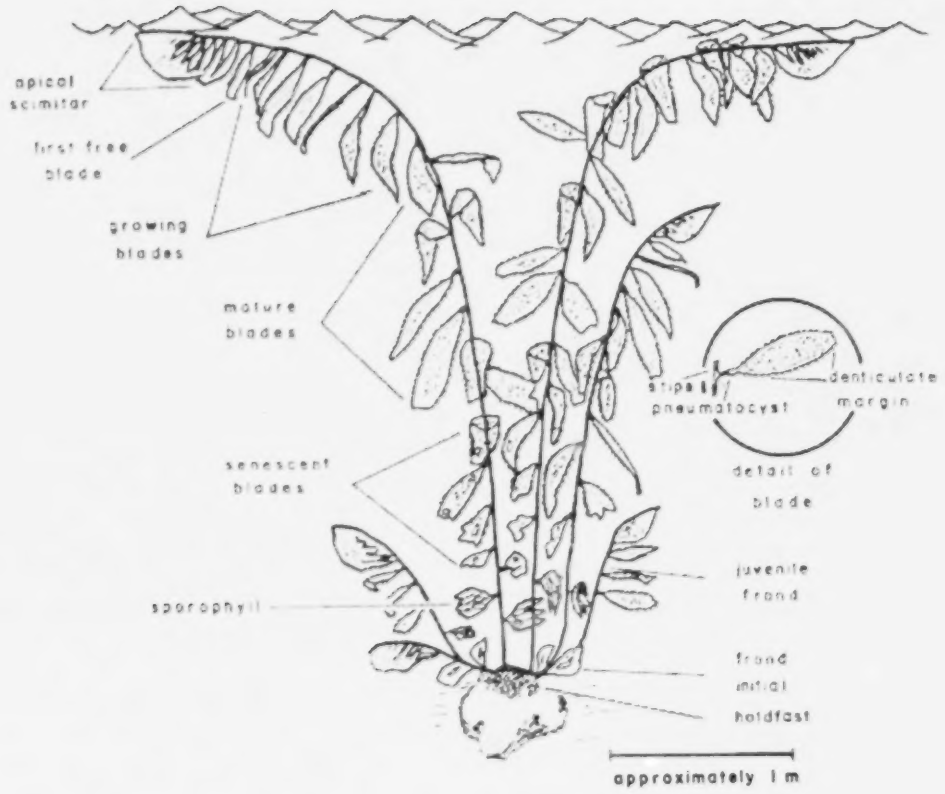


Figure 2. Semi-diagrammatic sketch of *Macrocystis integrifolia* Bory.

to produce the first frond initials and the apical scimitar (Figure 2). The apical scimitar continues dividing unilaterally to produce sporophylls (which divide producing many bladelets), blades and stipe. Once produced by this apical meristem, the blades continue to grow in length and width and the stipe continues to elongate. These tissues cease growing by the time the apical meristem has produced 1-2 m of new tissue distally. Blades consist of a flattened lamina and a pneumatocyst, which buoys the frond in the water. Mature laminae are 25-100 cm long and 7-15 cm wide, with irregularly bullate surfaces and a denticulate margin. Mature blades produce most of the photosynthate of the plant and export a portion of this to meristematic sinks at the growing end of the frond and to juvenile fronds and frond initials (Lobban, 1978c). Blades begin to senesce (deteriorate) two to three months after initiation (separation from the apical scimitar). Production of new tissues slows as the frond approaches the surface of the water and ceases at a length of about twice the depth of the holdfast below 0 tide (Lobban, 1976, 1978a).

Each of the frond intitials from the two primary fronds can divide to produce a new frond, each bearing two frond initials at their base; these, in turn, can produce new fronds. Thus, *M. integrifolia* has an indeterminate growth strategy and a series of fronds of various ages occurs on any mature plant. As many as 200 stipes may arise from one holdfast, but the average is in the range of 10 to 20 stipes.

Lobban (1978b) found that about 20 fronds could be potentially produced by one plant during the growing season in Barkley Sound, B.C. However, loss or suppression of growth of frond initials resulted in less than half the maximum number of fronds per plant. The life span of fronds produced during summer was about 6 months, but fronds produced in August could overwinter and complete growth in spring, thus living up to 10 months.

The perennial nature of the *Macrocystis* holdfast, when combined with: (1) the plant's propensity for producing new fronds, (2) the basal location of reproductive tissue, (3) large thallus, and (4) relatively rapid growth, renders *M. integrifolia* particularly attractive to commercial harvesting and, in certain ways, makes easier the task of resource management.

METHODS AND MATERIALS

Three zones were delineated within the kelp bed at the study site, with the shallowest (3.6 m. below MWL) at the inner edge of the bed, the middle depth (4.4 m. below MWL) at the center of the bed, and the deepest (5.2 m. below MWL) at the outer edge of the bed (Figure 1). Three stations were located in each of these zones, and each station was randomly assigned one of three harvesting treatments: control (unharvested), early harvest (June 7), or late harvest (July 17). At each station, five plants were randomly chosen and tagged. Fronds of tagged plants at harvest stations were cut at 1.6 m below MWL and all nearby plants were similarly cut to prevent shading. Immediately following this cutting, eight fronds with intact apical scimitars (*i.e.* those fronds lesser in length than the cutting height above the seabed) were labelled on each of five plants at each of the harvest stations, for an initial sample size of forty fronds. Eight fronds of similar length were labelled on each of five plants at the control stations. All tagged fronds were of similar size (means for each station were between 40 and 105 cm. long). Initially, and at subsequent intervals of 8 - 33 days (Table 1), lengths of tagged fronds were measured by SCUBA divers using a cloth measuring tape. Measurements were made from the frond base at the holdfast to the tip of the apical scimitar. It was estimated that frond lengths greater than 50 cm. were measured within ± 10cm., and those less than 50 cm. within ± 5 cm. The number of laminae on each frond were counted and sporophyll presence or absence and condition were noted. Five cut fronds on each harvest plant were also tagged and subsequent condition noted. Additional short fronds were tagged and measured at the control and early harvest stations on July 26.

Frond growth rate and percent daily elongation were calculated for each frond at each growth period. Growth rate was calculated as:

$$GR = (L_t - L_o) / t$$

where L_o was the length of the frond at the beginning of the growth period and L_t was the length at the end of the period, and t was the duration of

the period in days. Following North's (1971) assumption that over short time periods growth rate is a geometric relation, percent daily elongation was calculated as:

$$E = (L_t/L_o)^{1/t} - 1 \quad \text{(North, 197}$$

For each growth period the percent daily elongation of fronds was regressed on the common logarithm of the average length of fronds between two consecutive measurements. The standard growth rate (G), the percent daily elongation of a 1 m frond (North, 1971), was then calculated. Fronds having a negative growth rate during any of the growth periods, or that essentially did not grow after tagging, were eliminated from all calculations since North (1971) states that these fronds would cause considerable distortion in regressions. No more than 11% of the fronds were thus eliminated at any station during any growth period. Since slow-growing fronds are eliminated from calculations, G is representative only of the actively growing, not the total, population of fronds. Standard growth rate is a comparative index of growth. It is used because the growth rate of fronds is related to frond length (Lobban 1978a), a factor which makes comparison of growth over time and space very complex. G affords us a singular term which can be used to represent the growth of a whole population of fronds.

Analyses of variance were employed to determine the significance of effects of harvesting, station location or depth of the kelp bed, and initial length of frond (less than or equal to 50 cm, and greater than 50 cm in length) on actual growth rates of fronds (not G). Only fronds living through the entire period covered by the analyses were used and slow-growing fronds were not eliminated. In this report the term "significant" refers to a probability of 0.05 and "highly significant" to a 0.01 probability of rejecting a true null hypothesis.

Station Number	Station Description		Growth Periods 1	2	3	4	5	
7	Inner	Early Control *	June 11	July 13	July 25	August 16	August 26	Sept. 15
1		Early Harvest *	June 8	July 10	July 22	August 14	August 22	Sept. 9
4		Late Harvest		July 17	July 28	August 18	August 28	Sept. 15
5	Middle	Early Control	June 12	July 15	July 26	August 16	August 26	Sept. 13
2		Early Harvest	June 9	July 12	July 23	August 14	August 22	Sept. 9
8		Late Harvest		July 19	July 28	August 18	August 28	Sept. 15
6	Outer	Early Control *	June 13	July 16	July 27	August 17	August 27	Sept. 6
3		Early Harvest *	June 10	July 11	July 24	August 15	August 23	Sept. 1
9		Late Harvest		July 18	July 29	August 19	August 29	Sept. 6

* Shorter fronds of these plants were tagged at the beginning of the 3rd growth period. Newly tagged fronds of the control plants acted as controls for the late harvest plants.

Table 1. Sampling dates, growth periods and station descriptions for the *Macrocystis* harvest study, carried out near Masset, Queen Charlotte Islands, in 1974.

RESULTS AND DISCUSSION

1. Frond Growth

A complete tabulation of frond length and blade number data for each sampling period is provided in Appendix I. All analyses reported herein are based on this data. Regression parameters of percent daily elongation versus mean frond length for all stations and calculated standard growth rates (G) are given in Appendix II.

G values for control plants in June were 5-6 cm/day for outer, 4-5 cm/day for mid-position, and 3-4 cm/day for inner stations (Figure 3). During July respective G values were 4.5-5.5, 5-6, and 4-5cm/day. In August G fell below 4 at all positions but when calculated using the shorter fronds tagged on July 26, this decline in growth rate was not as marked.

Lobban (1976, 1978a, 1978b) found that G values of *Macrocystis integrifolia* in Barkley Sound, B.C. rose from 3.9 in early May to 4.3 cm/day by mid-June and fell to 1.1 cm/day from August through October. He suggested that the sharp decline in G during August 1975, may have resulted from heavy epiphytism of the lower laminae of longer fronds by the hydroid *Obelia* and the encrusting bryozoan *Membranipora*. *Membranipora* has been found to decrease the light available to the laminae of *M. pyrifera* (Wing and Clendenning, 1971). G values calculated from the shorter fronds tagged at the beginning of the third growth period were higher possibly due to reduced epiphytism. Roland (1980) has shown that *Macrocystis* laminae in Barkley Sound become heavily epiphytised by *Obelia* and *Membranipora* only when mature and at a distance of 1.5 m or more from the apical meristem. At least from June through August, plants in the Queen Charlotte Islands appeared to grow faster than more southern Barkley Sound plants, this is possibly due to the increased day length experienced by these more northerly plants during the summer. *M. integrifolia* grows slo

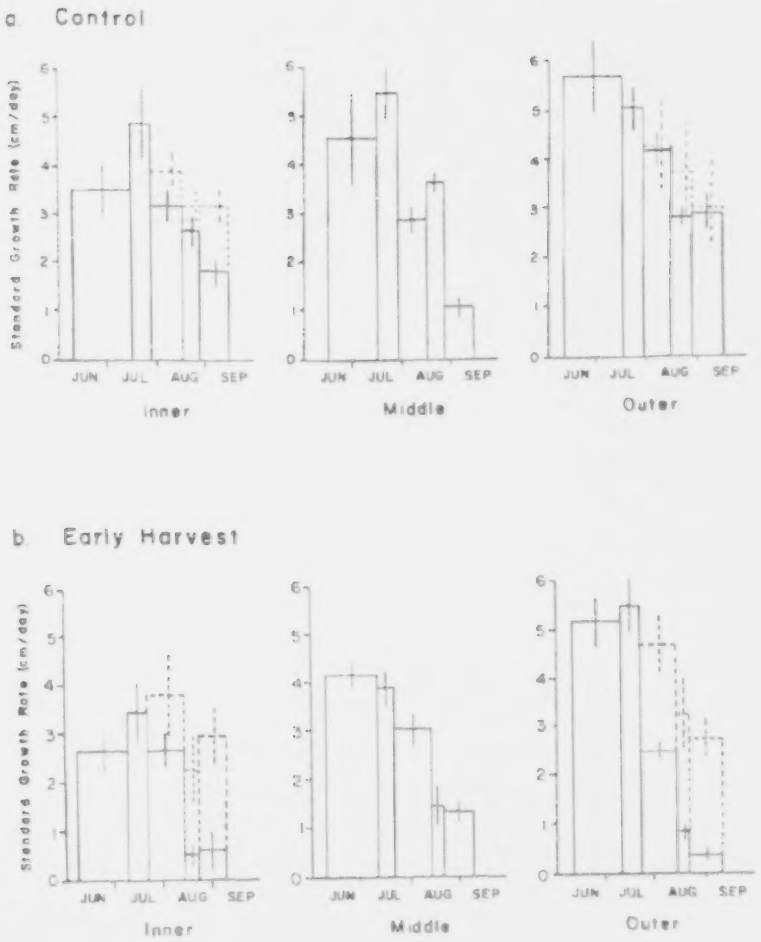


Figure 3. Standard growth rates (G) of fronds at inner, middle and outer control and early harvest stations throughout the entire study. Dashed lines indicate new fronds tagged about July 26. Vertical bars denote 95% confidence intervals about the mean.

than *M. pyrifera* which, in southern California, has G values averaging approximately 7 cm/day over the entire year (North, 1971).

The effect of station depth or position on growth rates was highly significant following the first harvest (Table 2), but not after the second harvest (Table 3). Following the first harvest, mean frond growth rates of control and harvested plants over the five growth periods were always lowest at the inner stations, and greatest at the outer stations (Figure 4). Druehl (1979) found that plants attached 4 m below zero tide level had frond elongation rates significantly slower than plants at -10 m. Whether the differences in growth rates observed in this study were related to depth cannot be determined since the depth difference was only 2m and the deeper stations were also further offshore, near the outer edge of the bed. Other major factors which may have influenced differential growth among the stations were water motion, nutrient availability, and light.

The initial size class of fronds (less than or equal to 50 cm and greater than 50 cm in length) significantly effected growth rates (Tables 2 and 3). Mean growth rates of small size class fronds were always less than the large size class fronds for any comparable treatment (Figure 4). This is in keeping with Lobban's (1978a) observations that exponential growth of fronds began only after a length of 50 cm was attained.

Harvesting in early June resulted in growth rates which were significantly lower than those observed at control stations (Table 2). All mean growth rates for both size classes of fronds were lower in harvest plants than in comparable controls (Figure 4). The effect was to decrease growth rate 1- 2 cm/day at all stations from growth periods 1 through 5. North (1968) observed full recovery of frond growth rates within 1 month on harvested *M. pyrifera* plants in southern California which had up to 55% of the biomass removed.

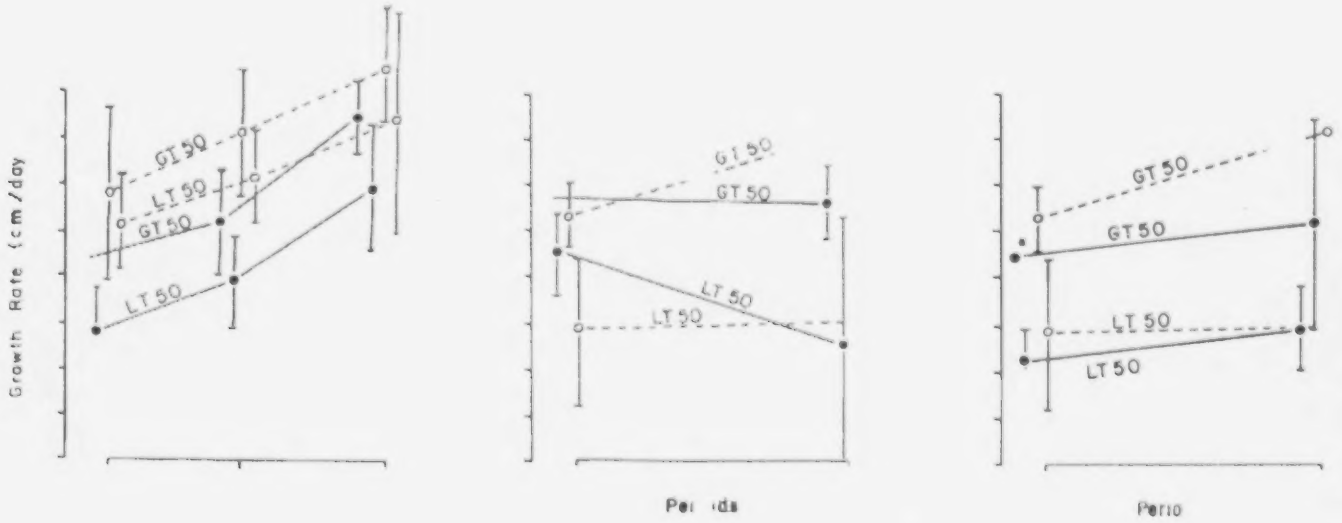
Harvesting on July 17 significantly affected growth rates (Table 3) from growth periods 3 through 5. Growth rates of these late harvested plants could not be compared with controls from the 2nd growth period

Table 2. Anova table testing the significance of position (inner, mid, outer), treatment (harvest, control), and initial size class of frond (less than or equal to 50 cm or greater than 50 cm) on fronds elongation rates following the first harvest. Data used were average growth rates of fronds following harvesting in early June through growth period 5.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main Effects	218.900	4	54.725	47.262	0.000
Position	10.000	2	5.000	27.157	0.000
Treatment	10.201	1	10.201	55.356	0.000
Initial	80.231	1	80.231	435.317	0.000
2-way Interactions	4.364	2	2.182	11.838	0.000
Position-Treatment	0.201	1	0.201	1.091	0.300
Position-Initial	4.097	1	4.097	22.232	0.000
Treatment-Initial	0.067	1	0.067	0.363	0.549
3-way Interactions	0.134	1	0.134	0.727	0.397
Position-Treatment-Initial	0.134	1	0.134	0.727	0.397
Explained	223.398	7	31.914	173.141	0.000
Residual	19.020	103	0.184		
Total	242.418	110	2.204		

Table 3. Anova table testing the significance of position (inner, outer), treatment (harvest, control) and initial size class of fronds (less than or equal to 50 cm or greater than 50 cm) on frond elongation rates following the second harvest. Data used were average growth rates of fronds following harvesting from growth periods 3 through 5.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main Effects	117.182	3	39.061	25.435	0.000
Position	0.550	1	0.550	0.364	0.537
Treatment	9.151	1	9.151	5.958	0.017
Sizeclass	69.230	1	69.230	45.072	0.000
2-way Interactions	19.902	3	6.634	4.319	0.007
Position-Treatment	12.309	1	12.309	8.014	0.006
Position-Sizeclass	12.433	1	12.433	8.094	0.006
Treatment-Sizeclass	4.295	1	4.295	2.861	0.095
3-way Interactions	0.167	1	0.167	0.109	0.742
Position-Treatment-Sizeclass	0.167	1	0.167	0.109	0.742
Explained	137.251	7	19.607	12.765	0.000
Residual	109.056	71	1.536		
Total	246.306	78	3.158		



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since additional small size class control fronds were not tagged until July 26. Fronds of control plants tagged early in June were too long by the second harvest for meaningful comparison. Following the late harvest, interactions between station position and harvesting treatment and between position and frond size class occurred. (Table 3). At the inner position mean growth rates of both size classes of fronds (particularly small size class fronds) were higher than comparable controls, but at the outer position mean regrowth rates were slightly less than controls (Figure 4). Following the early harvest, growth was clearly retarded in the harvested plants, but following the later harvest there was evidence of a slight enhancement from harvesting at the inner position. Moreover the difference between growth rates of control and harvested plants was much less in the deep plants following the later harvest than after the early harvest.

North (1968) reported that cutting fronds of *M. pyrifera* either caused a marked reduction in subsequent growth rates or an enhancement of growth, the effect realized being controlled by an interplay of increased light availability and the amount of blade tissue remaining on uncut fronds. Except under extremely turbid conditions, the immediate effect of canopy removal is an increase in light availability to juvenile fronds and the remaining blade tissue on cut fronds. North (1968) suggested that this may explain the enhanced growth of juvenile fronds sometimes observed after harvesting.

Lobban (1976, 1978c) has demonstrated that mature blades of both species of *Macrocystis* translocate photosynthate either upward to the apical scimitar and growing blades and/or downward to adjacent juvenile fronds. Removal of the apical scimitar of a mature frond of *M. pyrifera* caused a shift in the translocation pattern such that most of the translocate was exported down to the stipe of adjacent fronds (Lobban, 1977). Lobban (1976) presented data that suggested this effect may also occur in *M. integrifolia*, and he postulated that harvesting may enhance growth of juvenile fronds provided that sufficient numbers of mature blades remain on cut fronds.

The results of this study indicate that following the early

harvest, growth of plants at the inner position (which were cut closest to the sea bed) was no more retarded relative to their controls, than growth of the outermost plants; in fact, relative growth of these inner plants appears to have been enhanced by cutting July 17. These data suggest that the reduced amount of mature tissue remaining on the innermost plants was apparently compensated for by some mechanism, possibly increased light, such that the growth rate of these plants was not reduced relative to that of plants growing in water 1.4 m deeper. This observation may reflect for *M. integrifolia* the importance of the interplay of light availability and remaining blade tissue which was reported for *M. pyrifera* by North (1968). As will be demonstrated in a later section, the lengths of fronds remaining uncut after harvesting is critical to the rate of replenishment of the canopy.

2. Blade Production

The number of blades per length of stipe and the rate of production of blades are reported herein to characterize this north coast population and to evaluate the usefulness of these parameters for testing the effects of harvesting. The mean number of free blades (those released from the apical scimitar) per meter of stipe of control fronds 1-3 m long was 7.3 for inner, 5.8 for middle, and 5.2 for outer position plants for growth period 1 (Table 4); however, the difference in the number of free blades/m was non-significant ($p = 0.072$) between inner and outer positions. Druehl (1979) found that when *Macrocystis* plants were transplanted to deeper water the number of blades per mature frond remained essentially the same but that the distance between blades increased. Perhaps the lack of statistical significance in this study is due to the relatively small difference in seabed depth between inner and outer positions. The number of blades per meter of stipe changed little during the following two growth periods. Harvesting did not significantly effect the subsequent number of blades/m at any position (Table 4).

Table 4. Number of free blades/m of stipe for fronds averaging 1-3 m long on control and harvested plants at inner, middle and outer positions. Means and 95% confidence intervals are given. Means of control and harvested plants were tested after the first harvest by t-tests (ns = non significant).

		1st Growth Period	t s	Growth Periods 1 - 3
Inner	Control	7.3± 1.2 n = 13	1.46 (ns)	6.9± 0.9
	Harvest	8.4± 1. n = 15		7.7± 1.0
Middle	Control	5.8± 0.9 n = 17	1.43 (ns)	5.5± 1.2
	Harvest	5.2± 0.4 n = 17		6.0± 0.8
Outer	Control	5.2± 1.4 n = 11	0.09 (ns)	5.5± 1.2
	Harvest	5.3± 0.9 n = 9		5.9± 1.1

Mean blade initiation rates of control plants for periods 1-2 were 0.33/day at the inner, 0.27/day at the middle and 0.41/day at the outer position for fronds initially longer than 50 cm. For periods 3-5 mean rates were 0.23/day and 0.21/day respectively at inner and outer positions (Figure 5). These rates are similiar to those reported for other populations of *Macrocystis* in B. C. Sharp (1974) reported a mean rate of 0.4 blades/day for fronds 1-2 m long during August in Barkley Sound; values ranged from 0.2-0.7/day. Lobban (1976) reported rates of 0.22-0.35 blades/day in Barkley Sound from June 10-July 14, 1975.

The effect of harvesting on blade initiation rates was tested by t-tests (Sokal and Rohlf, 1969). At no position did harvesting significantly change blade initiation rates. However, as noted with the data for stipe elongation, a possible enhancement from harvesting is indicated in Figure 5 at the inner position following the second harvest. Fronds initially less than 50 cm in length had lower blade initiation rates than fronds initially greater than 50 cm in all but one case. It appears then that blade initiation rate is a less sensitive measure of growth than frond elongation rate.

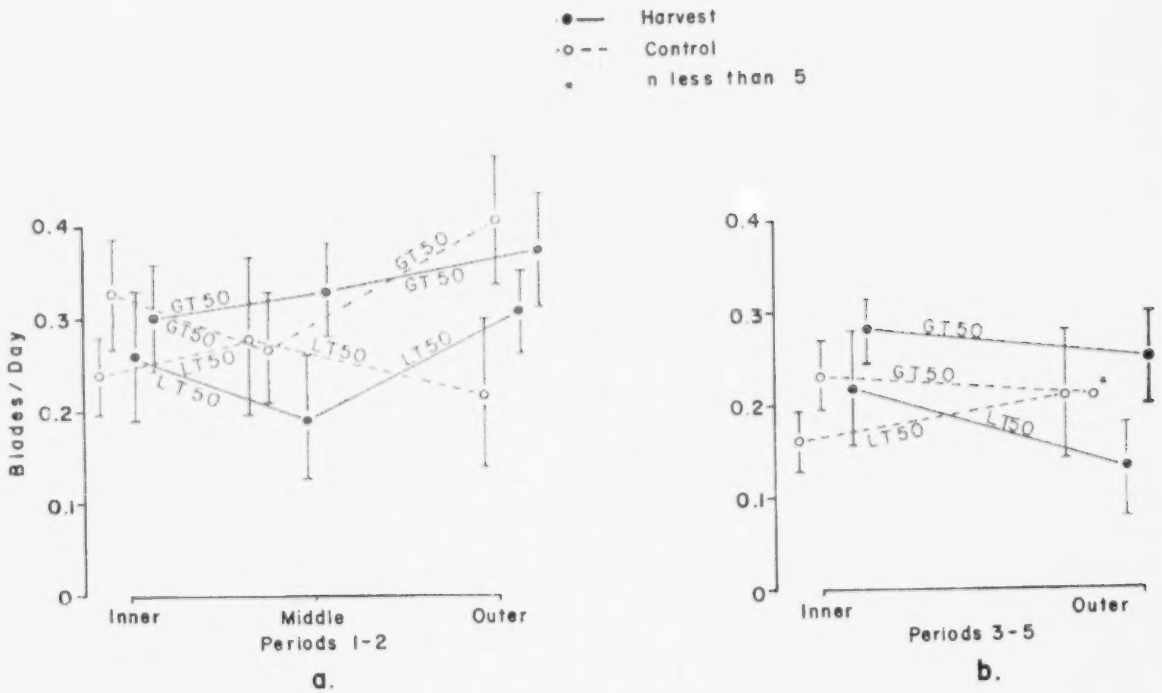

Figure 5. Blade initiation rates of control and harvested plants following the 1st and 2nd harvests. Means and 95% confidence intervals are plotted. GT = fronds initially greater than 50 cm in length. LT = fronds initially lesser than 50 cm in length.

REPLENISHMENT OF THE HARVESTED CANOPY

In the course of preparing this report we came to believe that the calculation of the canopy replenishment period might well provide a useful means of illustrating the impact of a particular harvesting treatment as well as estimating the potential for carrying out more than one harvest per year. Calculation of replenishment time to seasonally normal frond length distributions requires data of the following types:

1. the size class frequency of fronds following harvesting,
2. growth rates of various sizes of fronds following harvesting,
3. rate of frond recruitment on harvested plants,
4. rate of frond mortality on harvested plants,
5. size class frequency of fronds on unharvested plants at desired time for comparison with the harvested area, and the
6. rate of recruitment of new sporophytes into harvested areas.

The data gathered in this study provided growth rates of various sizes of fronds on harvested plants following harvesting (parameter 1); Average growth rates of fronds in one meter intervals derived from length (see Appendix II) are given in Table 5 for each growth period (parameter 2). Mean frond lengths were all initially less than 1.4 m. Growth rates were sometimes extrapolated beyond the data for a particular period since tagged fronds in a given size class were not always available for measurement.

Coon *et al*(1979) and Coon *et al* (in prep.) provided the size class frequency of fronds in September for the study area in 1976 and 1978 (parameter 5). According to pooled data of frond length distribution from Coon *et al* (1979) and Coon *et al* (in prep.), 44% of the sampled fronds would have formed a canopy at mean HHW (4.8 m above zero tide

Table 5. Growth rates of fronds (cm/day) throughout study for harvested plants. These rates were calculated from regression equations of percent daily elongation on Log_{10} mean frond lengths given in Appendix II. Rates were sometimes extrapolated beyond measured rates (*). ** = fronds tagged in growth period 3. Certain frond lengths were not available for measurement in all periods (-).

Following First Harvest

	Frond length (m)	Growth Period 1	2	3	4	5
Inner	1-2	3.6	4.1	5.4**	2.9**	4.2**
	2-3	5.2	5.4	5.1	3.8**	6.6**
	3-4	6.5*	5.8	6.4	2.7	3.4
	4-5	-	5.9*	7.5	3.6	4.5
	5-6	-	-	8.5*	-	5.5*
Middle	1-2	5.6	4.0	-	-	-
	2-3	7.9	4.9	5.0	-	-
	3-4	9.9*	5.1	5.7	4.0	-
	4-5	11.6*	5.1	6.0	4.8	-
	5-6	-	-	-	5.6	3.7
	6-7	-	-	-	6.4*	3.5*
Outer	1-2	7.1	-	7.2**	3.3**	4.0**
	2-3	10.9	9.2	-	6.1**	6.3**
	3-4	13.3	10.9	8.1	3.0	-
	4-5	15.5*	11.9*	7.8	3.8	5.1
	5-6	17.9*	12.1*	8.1	4.6	3.6
	6-7	-	12.6*	9.1	5.3	4.3
	7-8	-	-	-	6.1*	5.0*

Following Second Harvest

	Growth Period 2	3	4	5
Inner	6.1	4.2	4.2	-
	9.4	5.5	5.1	5.3
	12*	6.2	5.3	5.1
	-	-	-	4.9*
	-	-	-	4.7*
Middle	7.7	4.5	3.8	4.3
	13.9	7.2	5.4	5.6
	18.9*	9.7*	6.7	6.5
	-	12.7*	7.7*	7.0*
	-	-	-	-
	-	-	-	-
Outer	6.4	4.4	3.4	3.9
	9.8	6.9	4.8	4.8
	12.8	9.3	6.0	5.2
	15.7*	11.6*	7.0	5.1
	-	13.8*	7.9	4.7
	-	-	8.7*	4.8*
	-	-	-	-

level) in September (6 stations, n = 154 fronds).

We had no data pertinent to parameters 3, 4 and 6 and have assumed for purposes of this discussion that frond recruitment just balances the mortality of uncut fronds on harvested plants and that the recruitment of new sporophytes equals zero.

The time required for a 1 m long frond to reach a length equal to HHW was calculated by using the growth rate in Table 5. For the inner, middle and outer stations the estimated time was 89, 88 and 56 days respectively (Table 6). Following cutting at 1.6 m below mean water level the longest possible remaining uncut fronds at inner, middle and outer positions were 2.0, 2.8 and 3.6 m and the time required for each to reach HHW was calculated to be 55, 34 and 21 days, respectively. After harvesting on July 17, the time required for a 1 m frond to reach HHW at inner, middle and outer positions was 90, 76 and 95 days; the time estimated for the longest possible remaining fronds was 55, 28 and 30 days. Estimated rates following the second harvest were nearly equal for all positions because of the more similar and generally slow growth rates late in summer. The outstanding feature is the more rapid growth rate as longer fronds in exponential phase of growth are left uncut.

From the data provided by Coon *et al* (1979) and Coon *et al* (in prep.), we calculated that harvesting at 1.6 m below mean water level would have left 26% of the fronds in the bed uncut on plants attached 4-5 m below MWL. Thus, in order to reform a canopy at normal frond density, approximately 70% of the fronds would have to arise from frond initials, which are very slow growing. These data indicate that the times calculated for uncut fronds to reach HHW would provide the harvested area with only a sparse canopy by mid-September as most fronds would be submerged at HHW.

One other approach to estimating the impact of harvesting is to serially harvest a defined area and weigh the amount removed. This method directly measures canopy replenishment on the basis of biomass. The problem inherent with this technique is the variable distribution of kelp in the bed. Thus, unless large sample sizes are used, the use

of biomass to compare treated areas, or to determine seasonal changes in biomass is nearly impossible. For most studies then, only the magnitude of change between various treatments can be compared. These points are illustrated by the following study.

Coon and Lobban (unpublished) harvested 100 m^2 plots of *Macrocystis* near Port Hardy, B.C. in mid-June 1976, at 1.5, 3.0 and 4.5 m above the sea bed. Three plots were harvested in each case. The average depth of plots was 2.5 m below zero tide. They obtained initial yields ($\bar{x} \pm$ s.d.) of 307 $\pm$ 175, 206 $\pm$ 49 and 108 $\pm$ 28 kg, respectively, in these harvest plots. During a second harvest of the same plots in mid-August they obtained 73 $\pm$ 29, 105 $\pm$ 15 and 73 $\pm$ 9 kg respectively. These yields represent 26 $\pm$ 7%, 52 $\pm$ 10% and 70 $\pm$ 14% of the biomass removed in mid-June. Control areas were not harvested to estimate natural changes have probably been minimal.

With this type of study it is assumed that;

1) % change in biomass following a treatment is similar throughout the bed and independent of bed density; and that
2) % change in biomass in unharvested areas is never greater than for the least severe treatment. This assumption implies that harvesting does not enhance growth.

On this basis we would conclude that the density of kelp in unharvested areas did not decrease more than 30% (100-70) from June to August. Additionally we would conclude that at the two most severe treatments (cuts made at 1.5 and 3.0 m above the sea bed) the biomass was diminished at least 44% (70-26) and 18% (70-52), over the same period. Although differences between treatments were not significant at $P<0.05$, there is a clear trend which indicates that the canopy did not recover in the two most severe harvest treatment plots. Perhaps using a minimal treatment (such as cutting at 1 m below HHW) would suffice as a control to assess relative seasonal biomass changes in the beds instead of increasing sample size, which, in any event would likely be beyond the capacities

Table 6. Estimated time required to replenish canopy (growth to mean HHW) following harvesting June 9 and July 14, 1974.

Station position	Depth of bed below MHHW (m)	Depth of bed below 0 tide (m)	Longest possible frond remaining following harvesting (m)	Time required for longest possible frond remaining following harvesting to reach HHW (days)		Time required for a 1m frond to reach HHW (days)	
				After June 9th cutting	After July 15 cutting	After June 9 cutting	After July 15 cutting
Inner	5.4	0.8	2.0	55	55	69	90
Middle	6.2	1.4	2.8	34	29	50	76
Outer	7.0	2.2	3.6	21	20	50	75

of most harvesting studies. While both this and the former method indicated that the canopy would not reach normal seasonal densities following harvesting it is difficult to judge which approach to assessing the impact of harvesting is most accurate. Which method to employ in a given field situation may well depend on the relative cost.

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Appendix I. Tabulation of frond length and blade number data for stations 1-9 and growth periods 1-5. These data represent only those fronds which persisted throughout the complete experimental period. All calculations in this report were based on these data. F.L. - frond length (cm), No. B. = number of blades; N.E. = no data entry; numbers in parentheses in blade number columns are numbers of missing blades.

Plant Number	Frond Number	Growth Period 1		2		3		4		5		
		F.L.	No.B.	F.L.	No.B.	F.L.	No.B.	F.L.	No.B.	F.L.	No.B.	F.L.	No.B.
		Station 1: Inner position, early harvest											
101	59	23	0	87	7	148	10	237	16(2)	250	12(7)	290	12(15)
	60	47	5	110	15	150	14	200	10(9)	207	7(14)	230	4(19)
	61	32	4	70	9	106	13	180	13(5)	200	12(8)	280	18(11)
	65	92	7	199	15	250	19	372	16(11)	400	12(14)	470	19(17)
103	35	131	5	300	17	360	25	455	20	487	17(14)	510	20(20)
	36	134	7	328	18	420	23	604	23	627	24(11)	710	27(24)
	38	136	6	223	12	310	14	487	25	543	20(8)	770	21(15)
104	18	64	2	122	9	185	12	287	17(1)	290	12(5)	290	5(13)
	20	104	8	182	13	230	20	338	16(20)	347	13(14)	370	16(11)
	21	81	3	163	10	205	15	364	19(6)	376	17(10)	480	20(15)
105	75	26	0	75	5	123	10	251	15(1)	276	19	370	17(6)
	77	68	2	145	10	195	16	320	20(6)	335	18	400	18(15)
	78	41	1	88	10	131	13	251	14(8)	260	17	310	19(13)

Appendix I. (con't)

Plant Number	Frond Number	Growth Periods 3 F.L	3 No.B.	4 F.L	4 No.B	5 F.L.	5 NoB.	F.L	No.B.
		Station 1: Inner position, early harvest plants, (new fronds tagged at the beginning of the 3rd growth period).							
101	532	72	8	162	15	174	15(2)	265	9(12)
	535	10	0	43	7	120	7	120	9
	536	25	1	70	11	80	11	150	13
102	547	18	0	69	8	90	8	190	12
	548	25	0	90	8(1)	112	9	200	8
	549	23	0	90	8(1)	120	7(2)	220	13
	550	40	1	102	10	129	9	220	15
	551	52	2	91	10	110	9	180	12
105	553	16	0	30	8	36	7	61	11
	554	10	0	33	7	50	9	110	8
	557	49	5	109	11	126	12	200	14
104	537	90	5	200	15	234	17	340	19(5)
	538	50	6	90	11	95	10	110	7(4)
	539	40	2	70	12	81	12	120	9(3)
03	543	115	0	270	16(1)	293	16(3)	420	19(6)
	544	14	0	26	2(1)	30	2	50	6
	546	33	1	65	9	77	7(1)	100	7(1)

Appendix I (con't)

Plant Number	Frond Number	F.L	Growth Period 1 No.B	1 F.L.	2 No.B	2 F L	3 No.B.	3 F.L.	4 No.B	4 F.L.	5 NoB.	5 F.L.	No.B.
					Station 2 Middle position, early harvest								
201	84	63	3	286	14	384	19	404	22(9)	489	22(10)	660	22(7)
	85	96	5	345	17	437	22(2)	647	27(6)	668	29(13)	770	25(22)
	86	11	0	124	4	200	9	370	17(2)	384	20	595	18(19)
202	120	24	0	90	3	136	10	235	17	253	18	330	17(13)
	122	68	7	235	14	296	19	426	23(5)	438	25(7)	530	25(16)
	123	60	6	154	13	200	17	299	18(13)	304	15(10)	380	15(15)
	124	21	0	74	4	100	9	188	13	197	17	250	13(7)
	127	16	0	66	6	108	10	196	15(1)	211	17	280	18(4)
203	135	115	8	290	15	357	19	430	12(15)	443	12(15)	590	14(20)
	136	69	5	192	13	248	32	347	16(7)	361	15(13)	410	13(21)
	137	136	7	305	19	366	21(4)	465	21(12)	470	13(21)	510	14(20)
	138	152	9	350	19	418	23	489	17(16)	508	17(18)	560	14(26)
204	94	84	7	300	12(1)	390	18(1)	575	27(2)	595	26(8)	630	31(17)
	95	105	4	283	15	350	20	470	25(6)	489	18(13)	540	23(12)
	96	126	6	344	17	425	21	525	26(7)	529	18(17)	560	11(21)
	97	83	6	275	15	350	19	434	27(3)	458	23(8)	500	21(14)
	98	49	3	193	10	260	13	378	17(3)	392	19(3)	490	13(7)
	99	39	0	169	10	232	13	307	12(2)	319	19(3)	345	7(8)
	100	68	3	224	14	305	18	434	23(4)	461	11	560	25(10)

...(con't)

con't

Plant Number	Frond Number	Growth Period 2 F.L.	2 No.B.	3 F.L.	3 No.B.	4 F.L.	4 No.B.	5 F.L.	5 No.B	6 F.L.	6 No.B.	7 F.L.	7 No.B
					Station 2: Middle position, early harvest (con't)								
205	101	62	5	244	13	330	16	493	25(4)	518	27(4)	670	25(13)
	108	47	3	152	7	228	12(1)	298	18(3)	309	14(11)	380	12(25)
	110	23	0	115	4	173	13	275	15(2)	293	16(5)	350	15(12)
	111	65	6	223	11(2)	310	15	413	14(15)	417	15(13)	430	13(22)
	113	99	6	305	15	397	22	519	20(7)	546	29(8)	630	23(21)

Appendix I con't)

ant mber	Frond Number	F.L.	Growth Period 1 No.B	1 F L	2 No.B	2 F.L	3 No.B.	3 F.L	No.B	F.L	No.B	F L	No.B
					Station 3 Outer position, early harvest								
01	171	81	7	405	21	575	27	815	38(8)	912	44(8)	990	24(36)
	172	198	12	602	27	735	36	965	52(11)	998	43(19)	1070	32(40)
	173	44	2	283	20	475	21	723	38(1)	762	43(2)	880	34(15)
	174	61	6	246	12	391	21	600	32(6)	640	30(6)	730	30(19)
	175	49	5	201	13	350	20	565	21(5)	624	21(10)	710	14(27)
02	181	94	5	394	20	515	23	700	29(11)	745	33(11)	860	35(21)
	182	30	1	167	8	285	16	440	25	490	26	580	20(10)
	183	29	2	175	7	310	15	475	17	500	24(4)	540	20(14)
	185	174	9	540	25	675	39	877	37	929	45(10)	1040	40(24)
03	158	106	8	353	17	497	21	648	22(7)	670	25(12)	750	23(19)
	159	37	2	189	10	300	13	450	20(4)	497	22(6)	580	19(13)
	160	21	1	153	7	265	15(1)	391	16(3)	430	18(4)	490	15(9)
	161	182	11	442	20	567	27(3)	715	30(13)	753	27(17)	760	17(29)
	162	56	5	176	9	267	15	380	14(6)	419	13(9)	460	12(13)
	164	98	4	335	14	509	22	595	40(11)	631	29(16)	740	17(25)
	165	46	0	165	7	242	11	365	17(5)	387	22	460	13(27)
04	195	59	4	280	12	418	15	588	27	626	27(2)	710	23(17)
	196	191	12	463	19(4)	574	14(7)	710	27(10)	720	22(12)	970	24(23)
	198	70	4	293	12	433	19	615	24(5)	670	27(6)	710	17(12)
	199	73	4	292	12	436	17	583	17	624	24(7)	700	22(17)
05	146	71	7	265	13	375	17	540	22(5)	590	26(7)	711	27(11)
	147	150	7	480	21	622	27	750	22(7)	770	31(12)	850	22(27)
	148	53	3	137	10	367	15	560	19(7)	599	20(6)	720	22(12)
	149	79	5	290	12	410	16	604	25(7)	642	23(7)	750	13(20)
	150	44	4	274	12	403	15	560	14(5)	644	26(7)	753	29(10)
	151	34	1	134	8	210	11	271	12(1)	275	6(5)	280	12(12)

Appendix I (Con't)

Plant Number	Frond Number	Growth Period 3 F.L	3 No.B.	3 F.L	4 No.B.	4 F.L.	No.B.	F.L.	No.B.
		Station 3: Outer position plants, early harvest (new fronds tagged at the beginning of the 3rd growth period)							
301	588	40	2	120	9	170	12	290	19
	560	30	1	90	9	115	9	170	10
	561	28	0	91	9	126	13(1)	240	16
302	573	12	0	40	6	56	6	100	8
	574	60	4	162	12	185	12	330	17
	575	63	1	183	9	233	14	380	21
	576	30	0	88	10(1)	122	10(1)	220	13(1)
	577	63	0	183	10	250	16	400	17
303	568	62	6	132	10	145	11	180	7(4)
304	563	11	0	29	7	48	2	90	4
	567	70	6	180	10(1)	46	6	300	12
	578	33	2	105	10	137	9(1)	213	15
	579	21	0	80	5(2)	107	4(4)	160	5(3)
	580	28	1	60	8	79	10	151	12
	581	20	0	N.E.	N.E.	60	7	95	9

Appendix I (Con't)

Plant Number	Frond Number	F.L.	Growth Period 2 No.B	2 F.L	3 No.B.	3 F.L.	4 No.B.	4 F.L.	5 No.B.	5 F.L.	No.B.
			Station 4: Inner position, late harvest								
401	336	89	7(1)	132	9	215	20	250	18(2)	310	21(9)
	337	23	2	39	4	97	12	140	12	230	19
	339	16	1	25	3	58	10	80	12(2)	160	13(2)
	340	114	10	185	12	275	21	295	19	370	24(8)
	341	50	4	69	8	113	14	150	12	235	16(2)
	342	20	2	42	4	90	13	130	13	230	13(1)
	343	138	12	230	16	351	23	399	24(8)	480	30(12)
402	351	16	1	22	2	50	4	70	8	143	10
	352	115	6	155	8	252	18	290	15(4)	380	19(9)
	354	250	19	343	23	467	30(5)	510	31(6)	580	16(10)
	356	54	4	84	8	185	13	230	13	300	13(6)
	357	75	6	105	8	193	15(1)	240	15	335	20(4)
403	364	65	3	111	8	193	13(1)	248	12	340	15(7)
	367	50	3	109	6	192	12	235	11(2)	315	17(1)
	368	50	1	91	6	186	11	248	16	340	18(3)
	369	50	2	88	3	194	7(1)	240	10(1)	340	18(1)
	371	47	2	91	3	190	13	240	16	320	17
404	377	206	11	281	17	390	21(2)	440	17(3)	540	22(12)
	379	20	0	37	2	81	8	120	9	254	12
	381	166	8	N.E.	N.E.	376	21	440	22(1)	560	15(10)
	382	110	5	174	6	260	15	320	12	400	20(5)
	384	56	3	94	5	160	11	210	11	330	13(4)
405	394	60	2	103	5	192	14	250	14	360	15(4)
	395	71	2	109	8	212	12	240	14(1)	360	12(6)
	397	11	0	23	1	61	6	95	6	190	13

Appendix (Con t)

Plant Number	Frond Number	F.L.	Growth 10d										
			No.B.	F.L.	No.B				No.B				
			Station 2:				middle position, early control						
501	281	125	7	375	15	480	19	708	32	799	37	880	36(8)
	282	44	3	200	12	275	15	465	20	552	24	650	26(4)
	283	120	7	396	20	510	22	720	32	806	26	920	40(8)
	284	62	5	235	10	335	14	523	19	602	27	720	27(7)
	285	110	7	394	21	497	19	664	33	726	35	980	36(8)
502	256	37	4	162	14	235	14	392	21	485	28	610	34(5)
	257	34	3	159	13	297	15(1)	383	17(1)	465	20(3)	580	27(11)
	258	43	3	167	11	245	17	382	20	444	27	680	26(8)
	260	102	4	333	N.E.	410	22	574	25(1)	605	32(6)	750	35(12)
503	274	90	5	309	14	410	25	620	28(6)	671	30(6)	810	35(12)
	277	45	0	196	11	290	13	450	19	522	27	660	24(10)
	279	89	7	304	13(1)	395	17(1)	571	24(1)	622	25(7)	710	28(12)
504	266	170	12	305	20	367	19(5)	411	19(12)	466	15(25)	500	12(22)
	267	30	0	145	2	220	10	338	18	387	21	440	20(6)
	268	172	8	480	21(1)	560	26(2)	694	26(7)	720	31(8)	830	30(16)
	269	106	7	330	15	437	19	557	26(3)	616	26(5)	720	26(9)

Appendix (Cont'd)

Growth rate

Plant Number	Frond Number	F.L.	No.B.	F.L.	No.B.	F.L.	No.B.	F.L.	No.B.	F.L.	No.B.	F.L.	
						Station 6: Outer position, early control							
601	330	63	3	342	12	460	22	718	32	850	36	1039	43
	332	101	5	426	17	565	25	850	38	990	38	1150	45(6)
	333	28	1	195	11	302	13	530	25	660	26	760	35
	334	44	2	245	10	343	11	600	25	710	27(1)	925	37
602	308	69	5	256	16	327	20	452	23(2)	500	26(2)	595	27(5)
	313	10	0	84	4	148	21	300	16	375	16(1)	615	26
604	322	173	11	527	24	690	31	909	44(3)	930	32(17)	1117	36(16)
	323	143	6	436	17	571	25	800	37(3)	890	37(6)	961	39(10)
	325	67	3	310	15	436	18	568	34	770	37	955	48(2)
	326	53	3	275	12	393	16	598	28	660	26	751	26(5)
	327	237	14	648	32	784	41	1040	45(5)	1110	40(12)	1165	42(3)
	328	45	3	229	8	384	16	540	26(1)	560	19(2)	620	20(2)
605	296	83	9	422	21	543	27	700	29(9)	755	29(10)	820	21(23)
	297	60	4	285	12	390	16	552	29(1)	612	37	705	33(6)

Appendix I(Con't)

Plant Number	Frond Number	Growth Period 3 F.L.	3 No.B.	4 F.L.	4 No.B.	5 F.L.	5 No.B.	F.L.	No.B.
		Station 6: Outer position, late control (fronds tagged at 3rd growth period)							
602	628	43	0	102	8	140	7	218	14
	629	16	0	50	4	80	3	161	8
	630	36	0	110	8	148	7	275	12
	631	100	4	237	14	296	12	357	12
	632	16	0	45	4	75	5	153	9
603	634	145	6	335	14	410	19	626	25
	635	15	0	50	2	70	3	160	7
605	623	35	25	70	11	114	10	122	9
	626	30	16	50	5	70	5	131	9

Appendix I (Con't)

Plant Number	Frond Number	F.L.	Growth Period 1 No.B.	1 F.L.	2 No.B.	2 F.L.	3 No.B.	3 F.L.	4 No.B.	4 F.L	No.B.	F.L	No.B
				Station 7: Inner position, early control									
701	214	68	4	234	15	347	18	558	21(3)	651	29(7)	651	29(3)
	215	62	10	173	15	210	15	429	19(9)	489	18(14)	489	29(15)
702	219	19	1	90	11	163	12	290	19(2)	380	20(5)	380	23(9)
	233	58	5	175	11	254	16(1)	393	29(2)	440	24(4)	440	24(11)
	234	63	2	162	10	233	13	364	20(2)	408	16(4)	408	23(16)
	238	22	1	75	5	135	10	236	14	289	17	289	18(4)
703	239	20	2	88	6	167	12	273	14	333	21	333	24
	242	32	1	87	6	137	10	222	16	250	14(2)	250	11
	243	85	6	229	17	328	23	488	26(5)	551	31(7)	551	36(12)
	244	63	4	193	18	294	23	458	28(9)	515	27(9)	515	29(17)
	245	30	0	101	7	160	14	317	18	364	25(2)	364	23(10)
704	220	257	12	510	40	681	39(2)	840	35(7)	880	37(16)	880	30(21)
	225	40	4	154	7	256	16	421	17(1)	495	27(2)	495	26(14)
	228	43	11	259	15	318	22(5)	404	22(10)	430	24(19)	430	15(16)
705	251	22	0	99	5	99	11	323	15	420	15	420	28

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Appendix I (Con't)

Plant Number	Frond Number	F.L.	Growth Period 2 No.B.	2 F.L.	3 No.B.	3 F.L.	4 No.B.	4 F.L.	5 No.B.	5 F.L.	No.B.
			Station 8: Middle position, late harvest								
801	467	31	1	53	1	136	9	174	6	290	15
	468	13	0	15	0	33	5	44	5	79	6
	472	82	7	140	7	262	15	320	15	430	26
	473	163	8	226	12	350	20	390	22	490	23(7)
	474	10	0	10	0	22	2	31	3	60	4(3)
802	483	48	1	77	0	197	11	250	16	390	23
	486	160	6	226	11	340	18	398	13	520	20(10)
803	497	107	3	159	6	305	18	390	25	520	29
	498	21	0	34	0	63	9	100	8	185	13
804	506	64	3	96	3	201	12	265	17	365	18(3)
	510	103	5	148	5	281	15	340	12	420	19(4)
	513	20	0	29	0	47	4	71	8	170	9
805	520	37	0	60	0	136	10	175	11	270	19
	525	28	0	47	4	75	18	90	8	180	9
	526	158	5	211	10	327	19	380	19	490	24

Appendix I (Con't)

Growth Period

Plant Number	Frond Number	2 F.L.	2 No.B.	3 F.L.	3 No.B.	4 F.L.	4 No.B.	5 F.L.	5 No.B.	6 F.L.	6 No.B.
					Station 9: Outer position, late harvest						
901	403	157	6	243	5	410	14	460	19	540	19(1)
	405	35	0	65	1	N.E.	N.E.	202	8	280	6
	406	35	0	64	0	147	7	203	9	270	11(1)
	407	123	3	184	5	329	14	360	14	420	17
	408	200	7	296	10	470	19	553	25	650	24(1)
	409	16	1	121	3	253	8	308	12	380	11
	410	45	1	70	1	153	6	197	9	270	7
902	417	13	0	20	0	N.E.	N.E.	59	4	100	5
	419	212	7	312	13	487	19	555	25	570	13(11)
	421	22	0	29	0	64	8	89	9	250	9
	423	123	7	217	7	374	17	450	21	450	16
903	430	213	10	330	11	480	20	540	25	610	31(1)
	431	14	0	25	0	48	5	64	5	100	8
	432	200	7	N.E.	N.E.	435	22	550	20	710	31
	433	60	3	100	3	240	14	294	17	430	20
	434	47	0	68	3	134	9	163	10	250	15
	435	191	10	277	10	456	21	520	24	610	30
904	445	129	6	190	6	360	14	414	24	530	24
	447	62	2	96	3	218	10	274	13	380	15
905	456	125	5	178	6	285	13	321	13	360	12(1)
	461	149	7	220	8	400	17(1)	464	21	560	24(2)
	462	345	15	440	18	573	25(2)	622	30	710	16(17)

Appendix II. Regression parameters of percent daily elongation versus Log_{10} mean frond length (cm), and calculated standard growth rates (G).

Station #	Treatment & Position	Growth Period	Dates (1974)	Slope (m)	y Intercept	G (y at logx=2)	95% Conf. Interval of G
	early harvest; inner	1	Jun 8 - Jul 10	-1.46	5.60	2.68	± 0.39
		2	Jul 10 - Jul 22	-3.26	9.96	3.43	± 0.64
		3	Jul 22 - Aug 14	-1.56	5.81	2.69	± 0.36
		4	Aug 14 - Aug 22	0.17	0.35	0.70	± 0.22
		5	Aug 22 - Sept 9	0.37	0.02	0.75	± 0.40
	early harvest; middle	1	Jun 9 - Jul 12	-2.41	8.96	4.13	± 0.50
		2	Jul 12 - Jul 23	-3.11	10.11	3.89	± 0.39
		3	Jul 23 - Aug 14	-2.66	8.35	3.03	± 0.33
		4	Aug 14 - Aug 22	-0.59	2.64	1.45	± 0.37
		5	Aug 22 - Sept 9	-0.89	3.12	1.34	± 0.23
	early harvest; outer	1	Jun 10 - Jul 11	-2.65	10.53	5.21	± 0.53
		2	Jul 11 - Jul 24	-4.41	14.32	5.51	± 0.56
		3	Jul 24 - Aug 15	-1.35	5.18	2.48	± 0.19
		4	Aug 15 - Aug 23	-0.11	1.13	0.91	± 0.14
		5	Aug 23 - Sept 11	0.37	-0.38	0.36	± 0.12
	late harvest; inner	2	Jul 17 - Jul 28	-1.49	7.34	4.37	± 0.65
		3	Jul 28 - Aug 18	-2.81	8.93	3.31	± 0.51
		4	Aug 18 - Aug 28	-3.57	10.59	3.45	± 0.49
		5	Aug 28 - Sept 16	-4.85	13.79	4.09	± 0.48
	early control, middle	1	Jun 12 - Jul 15	-0.91	6.39	4.56	± 0.96
		2	Jul 15 - Jul 26	-5.34	16.17	5.49	± 0.59
			Jul 26 - Aug 16	-1.76	6.39	2.88	± 0.32
		4	Aug 16 - Aug 26	-3.39	10.48	3.71	± 0.30
		5	Aug 26 - Sept 13	-0.01	1.10	1.07	± 0.28
	early control; outer		Jun 13 - Jul 16	-3.71	13.16	5.73	± 0.82
			Jul 16 - Jul 27	-3.99	13.07	5.09	± 0.69
			Jul 27 - Aug 17	-3.13	10.52	4.26	± 0.44
			Aug 17 - Aug 27	-2.00	6.87	2.87	± 0.41
			Aug 27 - Sept 16	-2.32	7.56	2.93	± 0.37
	late control; outer (retagged)	3	Jul 27 - Aug 17	-0.87	6.04	4.30	± 1.30
			Aug 17 - Aug 27	-3.03	9.77	3.70	± 1.35
			Aug 27 - Sept 16	-2.11	7.32	3.09	± 1.21
	early control; inner		Jun 11 - Jul 13	-2.40	8.33	3.52	± 0.58
			Jul 13 - Jul 25	-4.27	13.39	4.86	± 0.82
			Jul 25 - Aug 16	-2.09	7.37	3.20	± 0.38
			Aug 16 - Aug 26	-1.99	6.66	2.68	± 0.36
			Aug 26 - Sept 13	-0.73	3.28	1.81	± 0.39
	late control; inner (retagged)	3	Jul 25 - Aug 16	0.81	2.36	3.99	± 0.39
			Aug 16 - Aug 26	-0.49	4.11	3.13	± 0.48
			Aug 26 - Sept 13	-1.04	5.27	3.19	± 0.33
8	late harvest; middle	2	Jul 19 - Jul 28	0.78	3.44	5.00	± 0.86
			Jul 28 - Aug 18	-0.72	4.61	3.17	± 0.71
			Aug 18 - Aug 28	-1.80	6.49	2.89	± 0.78
			Aug 28 - Sept 16	-2.79	8.95	3.36	± 0.84
9	late harvest; outer	2	Jul 18 - Jul 29	-1.65	7.89	4.58	± 1.31
			Jul 29 - Aug 19	-0.78	4.65	3.10	± 0.50
			Aug 19 - Aug 29	-1.47	5.46	2.52	± 0.39
			Aug 29 - Sept 16	-3.16	9.51	3.20	± 0.63
	early harvest; inner (retagged)	3	Jul 22 - Aug 14	-1.09	5.95	3.78	± 0.85
		4	Aug 14 - Aug 22	-1.77	5.77	2.23	± 0.70
		5	Aug 22 - Sept 6	-0.82	4.60	2.95	± 0.60
3	early harvest; outer (retagged)	3	Jul 24 - Aug 15	0.29	4.16	4.74	± 0.60
		4	Aug 15 - Aug 23	-1.75	6.71	3.22	± 0.74
		5	Aug 23 - Sept 11	-0.48	3.68	2.72	± 0.41